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NEW SPECIES AND RECORDS OF BIRDS (AVES: MEGAPODIIDAE, COLUMBIDAE) FROM AN ARCHEOLOGICAL SITE ON LIFUKA, TONGA

David W. Steadman

Abstract.—A new species of megapode, *Megapodius alimentum,* is described from bones excavated at the Tongoleleka archeological site, Lifuka, Ha'apai Group, Tonga. Two coracoids from the same site are referred to *Megapodius* cf. *molistructor* and *Caloenas* cf. *canacorum,* both extinct species otherwise known from late Holocene fossils on New Caledonia. Another coracoid from Tongoleleka is referred to *Ducula* cf. *david,* an extinct species recently described from an archeological site on Wallis (Uvea) Island. A single tibiotarsus, too fragmentary to be named, represents an extinct, undescribed species of *Ducula* that is larger than any congener, living or extinct. The first four extinct species from Lifuka are more closely related to Melanesian species than to those of eastern Polynesia. The occurrence of five extinct species at the Tongoleleka site indicates that late Holocene losses of land birds in western Polynesia may have been as severe as those in eastern Polynesia.

In 1984, Tom Dye of Yale University excavated a rich archeological deposit on Lifuka, Ha'apai Group, Tonga, known as the Tongoleleka Site. Situated in an ancient sand dune, the site consists of three strata (Layers II, III, and IV) that bear pottery. The lowest and oldest stratum is stratigraphic Layer IV, which mainly represents Cultural Unit III. Layer IV, buried by 1 to 1.5 m of more recent sand, yielded decorated Lapita pottery, believed on the basis of sites excavated elsewhere to date at 3500 to 3000 years B.P. (T. Dye, pers. comm.). Two radiocarbon dates on charcoal from the upper portion of the overlying stratigraphic Layer III are 2260 ± 60 years B.P. (Beta-14171) and 1370 ± 70 years B.P. (Beta-11243).

Among the 20 identifiable bird bones from Tongoleleka are 11 bones of land birds, all but two of which are from stratigraphic Layer IV. Six of these bones are from two species of extinct megapodes, four others are from three extinct and one extant species of columbids, and one is from the extant starling *Aplonis tabuensis.* Also recovered were shellfish and bones of fish, reptiles, mammals, and marine birds. All of the bones probably represent food remains of early Tongans.

The purpose of this paper is to describe the morphology and systematics of the extinct species of birds from Tongoleleka. Additional details of the chronological, stratigraphic, zoogeographic, and cultural contexts of these extinct species will be presented in a future publication.

Materials and methods.—The fossil specimens are cataloged in the vertebrate zoology collections of the Bernice P. Bishop Museum (BPBM). Modern skeletal specimens are from the Division of Birds, National Museum of Natural History, Smithsonian Institution (USNM). Fossils from New Caledonia are from the Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris (MNHN). Osteological terminology mainly follows that of Baumel et

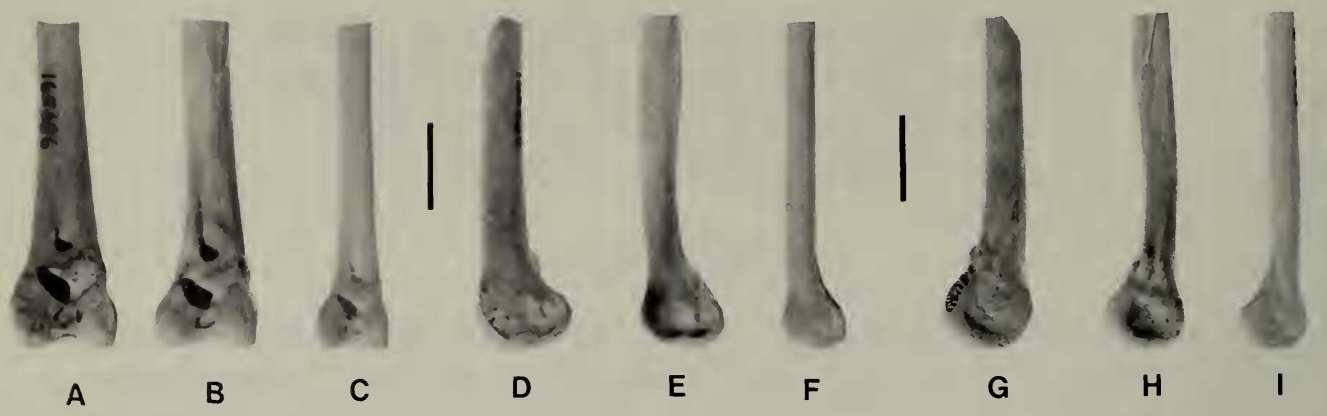

Fig. 1. The tibiotarsus of *Megapodius* in cranial (A–C), medial (D–F), and lateral (G–I) aspects. A, D, G, Holotype of *Megapodius alimentum,* new species, Lifuka, Tonga, BPBM 165686; B, E, H, *M. freycinet freycinet,* male, Halmahera, Northern Moluccas, USNM 557015; C, F, I, *M. pritchardi,* sex unknown, Niuafo'ou, Tonga, USNM 319633. Scale bars = 10 mm.

al. (1979). Measurements were taken with dial calipers with increments of 0.05 mm, rounded to the nearest 0.1 mm. CU = Cultural Unit.

Systematic Paleontology

Class Aves
Order Galliformes
Family Megapodiidae

Six specimens are referred to the Megapodiidae rather than to *Gallus gallus* of the Phasianidae, the only other galliform in Oceania, because of the following characters: coracoid–ventro-medial margin of humeral end of shaft more rounded, cotyla scapularis not extending beyond lateral margin of shaft in dorsal aspect, shaft (just sternal to cotyla scapularis) more rounded in cross-section; tibiotarsus—condylus medialis and condylus lateralis short and wide, epicondylus medialis large; tarsometatarsus—distal half of facies dorsalis convex rather than concave, tuberculum intercondylarum small, tuberositas musculo tibialis cranialis large and protruding dorsad to facies dorsalis, fossa metatarsi large and deep, extending beyond medial edge of facies dorsalis; pedal digit I, phalanx 1—large size, straight shaft; pedal digit II–IV, terminal phalanx—large size, dorso-ventrally compressed, medio-laterally expanded.

Genus *Megapodius*

Within the Megapodiidae, the fossils are referred to *Megapodius* (including *Eulipoa,* following Ripley 1960) rather than to *Leipoa, Alectura, Aepypodius, Tallegalla,* or *Macrocephalon* by the following combination of characters: tibiotarsus—distal margin of pons supratendineus nearly perpendicular (less diagonal) to the long axis of the shaft, ventral margin of condylus lateralis protrudes more ventrad from the shaft; tarsometatarsus—shaft wide but dorso-ventrally compressed, fossa metatarsi I distinct, deep, and circular in deeper portion, foramen vasculare distale large; pedal digit II–IV, terminal phalanx—dorso-ventrally compressed, medio-laterally expanded.

Megapodius alimentum, new species
Figs. 1–3

Holotype.—Distal end of tibiotarsus, BPBM 165686, Pit 0N0W, Layer IV (CU-III), Tongoleleka archeological site (To-Li), Lifuka, Ha'apai Group, Tonga. Tom Dye and field party Aug 1984.

Paratypes.—All from Tongoleleka site. Proximal end of tarsometatarsus, BPBM 165689, Pit 0N0W, Layer IV (CU-III). Tarsometatarsus lacking both ends, BPBM 165670, Pit 45N1W, Layer IV (CU-III).

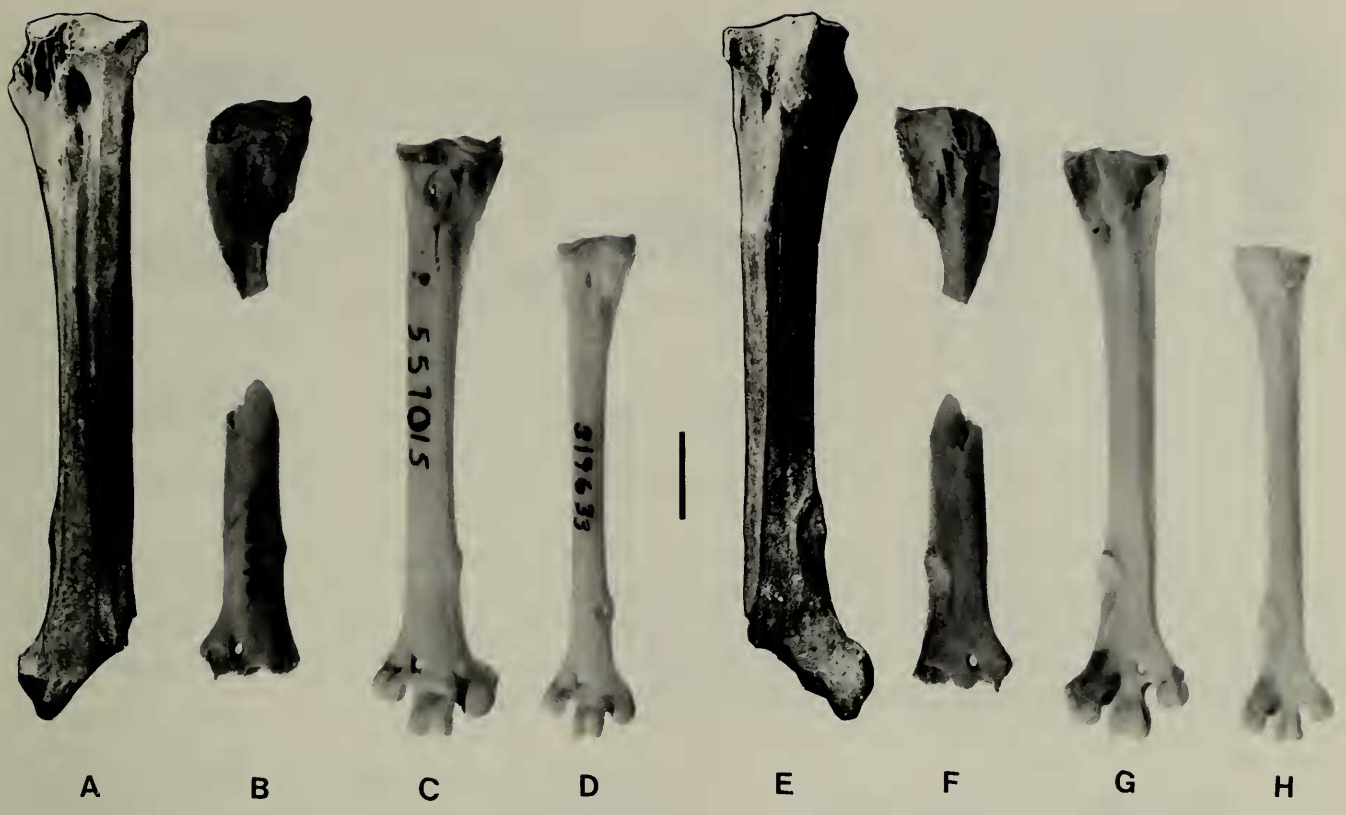

Fig. 2. The tarsometatarsus of *Megapodius* in dorsal (A–D) and plantar (E–H) aspects. A, E, Holotype of *M. molistructor,* New Caledonia, MNHN 600; B, F, Paratypes of *M. alimentum,* new species, Lifuka, Tonga, BPBM 165689, 165670; C, G, *M. freycinet freycinet,* male, Halmahera, Northern Moluccas, USNM 557015; D, H, *M. pritchardi,* sex unknown, Niuafo'ou, Tonga, USNM 319633. Scale bar = 10 mm.

Pedal digit I, phalanx 1, BPBM 165674, Pit 0N11W, Layer IV pit (CU-III). Pedal digit II–IV (exact number uncertain), terminal phalanx, BPBM 165675, Pit 0N11W, Layer IV pit (CU-III).

Diagnosis.—A large species of *Megapodius,* exceeded in size only by *M. molistructor* (Tables 1–3). *Megapodius alimentum* differs from *M. freycinet* as follows: tibiotarsus—incisura intercondylaris wider, tuberositas retinaculi musculo fibularis larger and more distinctly offset from condylus lateralis; tarsometatarsus—foramina vascularia proximalia more deeply inset below the dorsal surface of facies dorsalis, lateral margin of facies dorsalis more rounded at level of foramina vascularia proximalia; digit I, phalanx 1—stouter; digit II–IV, terminal phalanx—broader medio-laterally. *Megapodius alimentum* differs from *M. molistructor* in the same characters of the tarsometatarsus, as well as in the smaller foramina vascularia proximalia and the less prominent crista plantare medialis. *Megapodius alimentum* differs from *M. pritchardi* in the same characters of the tibiotarsus and phalanges, but not those of the tarsometatarsus.

Etymology.—From the Latin *alimentum,* meaning "food." The name *alimentum* refers to the presumed eating of this species by the early Tongans who deposited the bones at Tongoleleka.

Remarks.—Although modern skeletons were not available for *Megapodius laperouse* of Micronesia (Palau, Marianas), measurements of skins (Baker 1951:106–113) indicate that *M. laperouse* is smaller than *M. freycinet freycinet,* and therefore would be significantly smaller than *M. alimentum.* In spite of their large difference in size (Tables 1–3), the qualitative similarity between the tarsometatarsi of *M. alimentum* and *M. pritchardi* suggests that the former may be more closely related to *M. pritchardi* than to *M. freycinet.*

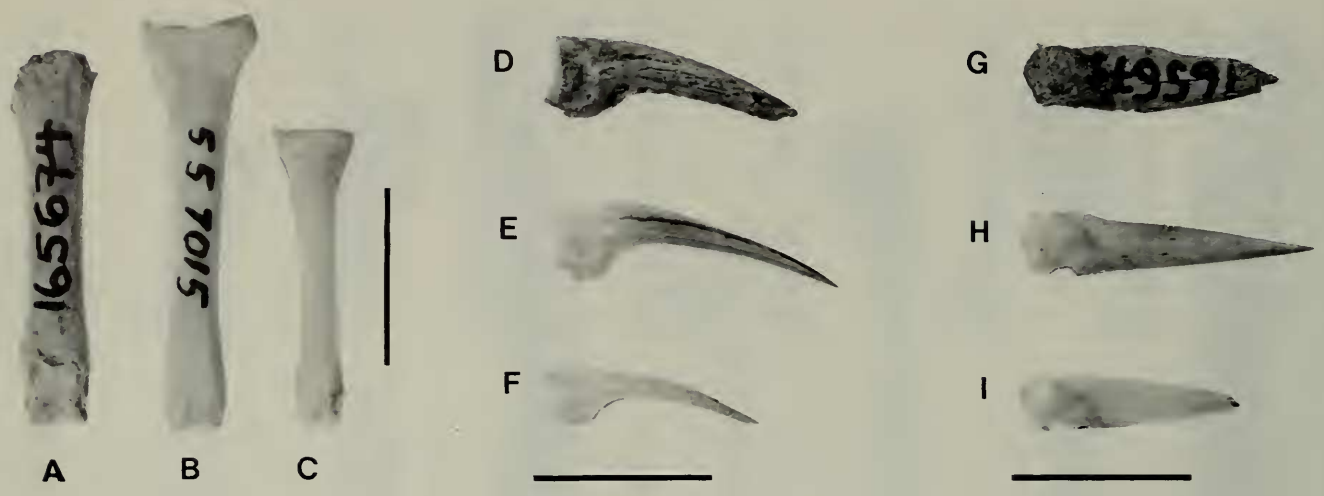

FIG. 3. The digit I, phalanx 1 in dorsal aspect (A–C) and digit II–IV (exact number uncertain), terminal phalanx in lateral (D–F) and ventral (G–I) aspects in *Megapodius*. A, Paratype of *M. alimentum*, new species, Lifuka, Tonga, BPBM 165674; D, G, Paratype of *M. alimentum*, new species, Lifuka, Tonga, BPBM 165675; B, E, H, *M. freycinet freycinet*, male, Halmahera, Northern Moluccas, USNM 557015; C, F, I, *M. pritchardi*, sex unknown, Niuafo'ou, Tonga, USNM 319633. Scale bars = 10 mm.

Megapodius cf. *molistructor*
Balouet & Olson
Fig. 4

Referred material.—Humeral half of coracoid, lacking most of processus acrocoracoideus, facies articularis clavicularis, and processus coracoideus, BPBM 165682, Pit 0N11W, Layer IV (CU-III), Tongoleleka archeological site (To-Li), Lifuka, Ha'apai Group, Tonga. Tom Dye and field party Aug 1984.

Table 1.—Measurements (in mm) of the tibiotarsus in *Megapodius*, giving mean, range, and sample size. For sample sizes larger than 10, the mean is rounded to the nearest 0.05. F = female. M = male. U = sex unknown.

	Least width of shaft	Least depth of shaft	Distal width through condyles	Distal width through epicondylus medialis	Depth of condylus lateralis	Length through pons supra-tendineus	Width of incisura inter-condylaris
Megapodius alimentum	5.5	4.8	12.2	12.8	10.5	3.0	2.7
Holotype, BPBM 165686	1	1	1	1	1	1	1
Lifuka, Tonga (U)							
M. pritchardi	3.9	3.4	8.2	8.3	7.3	1.8	2.0
Niuafo'ou, Tonga (2U)	3.8–4.0	3.3–3.5	8.1–8.3	8.1–8.5	7.1–7.5	1.6–2.0	1.9–2.0
	2	2	2	2	2	2	2
M. freycinet freycinet	5.60	4.35	11.30	11.75	9.40	2.65	2.10
Halmahera, Moluccas	4.8–6.4	3.7–4.7	10.3–12.2	11.1–12.5	8.8–10.1	2.0–3.2	1.5–2.6
(12M, 10F)	22	22	21	21	20	22	19
M. freycinet pusillus	5.9	4.6	12.3	12.6	9.9	2.6	2.6
Philippines (M)	1	1	1	1	1	1	1
M. freycinet gilberti	4.6	3.8	9.4	9.6	8.2	2.2	1.6
Celebes (1M, 1F)	4.3–5.0	3.7–3.8	9.1–9.6	9.6–9.7	8.1–8.3	2.2	1.4–1.7
	2	2	2	2	2	2	2
M. freycinet abbotti	5.6	4.6	11.4	11.7	9.9	2.7	2.3
Nicobar Islands (2M)	5.3–5.9	4.5–4.7	11.3–11.6	11.3–12.1	1	2.5–2.9	2.2–2.4
	2	2	2	2		2	2

Table 2.—Measurements (in mm) of the tarsometatarsus in *Megapodius*, giving mean, range, and sample size. For sample sizes larger than 10, the mean is rounded to the nearest 0.05. The values for *M. molistructor* are estimations extrapolated from similar measurements in Table 3 of Balouet & Olson (in press b). FVP = foramina vascularia proximalia. F = female. M = male. U = sex unknown.

	Proximal depth to hypotarsal canal	Depth of lateral side of facies dorsalis at level of FVP	Width of shaft at proximal edge of fossa metatarsi I	Minimum width of shaft through fossa metatarsi I	Depth of shaft just proximal to fossa metatarsi I	Length of fossa metatarsi I
Megapodius alimentum	7.0	3.4	6.7	6.6	3.7	9.5
Lifuka, Tonga (U)	1	1	1	1	1	1
BPBM 165670, 165689						
M. pritchardi	4.4	1.9	4.2	4.3	2.4	5.9
Niuafo'ou, Tonga (2U)	4.3–4.4	1.8–2.0	4.2–4.3	4.2–4.4	2.3–2.5	5.6–6.2
	2	2	2	2	2	2
M. molistructor	ca. 7.7	—	ca. 8.7	ca. 8.9	ca. 4.4	—
New Caledonia (U)	1		1	1	1	
M. freycinet freycinet	5.80	2.45	6.10	6.25	3.25	8.85
Halmahera, Moluccas	4.8–6.3	1.7–2.9	5.5–6.8	5.6–7.0	2.9–3.6	7.9–9.6
(12M, 10F)	19	20	22	22	22	22
M. freycinet pusillus	6.2	2.6	6.4	6.7	3.5	9.6
Philippines (1M)	1	1	1	1	1	1
M. freycinet gilberti	4.8	2.4	5.0	5.2	2.7	7.9
Celebes (1M, 1F)	4.8	2.0–2.7	4.9–5.0	5.1–5.3	2.6–2.8	7.8–8.0
	2	2	2	2	2	2
M. freycinet abbotti	5.8	2.4	6.4	6.5	3.2	9.0
Nicobar Islands (2M)	5.8–5.9	1	6.2–6.5	6.2–6.8	3.1–3.4	8.7–9.2
	2		2	2	2	2

Table 3.—Measurements (in mm) of the digit I, phalanx 1 (DI, P1) and digit II–IV, terminal phalanx (DII–IV, TP) in *Megapodius*, giving mean, range, and sample size. For sample sizes larger than 10, the mean is rounded to the nearest 0.05. F = female. M = male. U = sex unknown.

	Length of DI, P1	Minimum width of DI, P1	Minimum depth of DI, P1	Maximum width of DII–IV, TP
Megapodius alimentum	21.2+	3.0	2.9	4.0+
Lifuka, Tonga (U)	1	1	1	1
BPBM 165674, 165675				
M. pritchardi	16.3	2.0	1.6	2.7
Niuafo'ou, Tonga (2U)	16.0–16.6	1.9–2.0	1.6–1.7	2.6–2.8
	2	2	2	2
M. freycinet freycinet	22.25	2.55	2.55	3.20
Halmahera, Moluccas	20.8–23.9	2.2–2.8	2.3–2.8	2.7–3.5
(12M, 10F)	21	22	22	22
M. freycinet pusillus	23.2	2.6	2.4	3.0
Philippines (1M)	1	1	1	1
M. freycinet gilberti	18.8	2.0	2.0	2.4
Celebes (1M, 1F)	18.3–19.3	1.9–2.1	1.9–2.0	1
	2	2	2	
M. freycinet abbotti	21.5	2.5	2.4	3.2
Nicobar Islands (2M)	21.5	2.5	2.3–2.4	3.0–3.5
	2	2	2	2

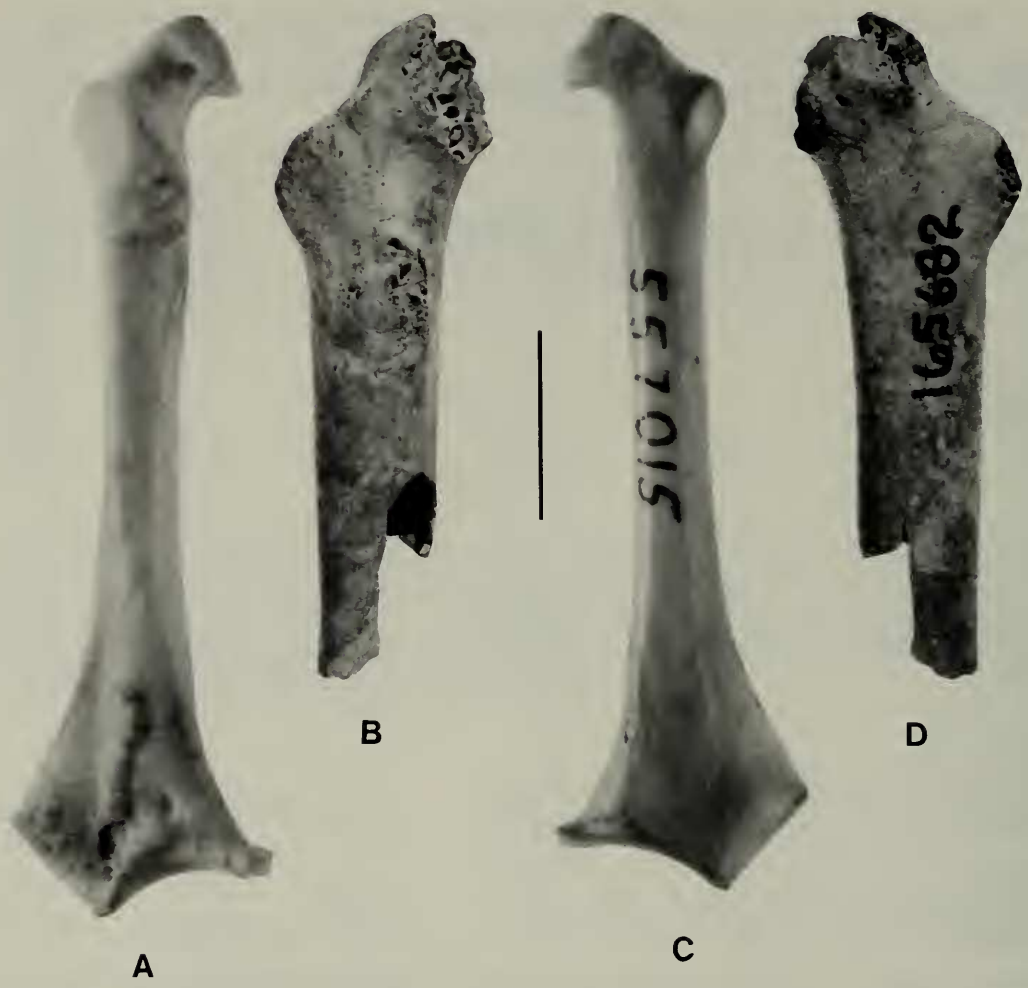

Fig. 4. The coracoid of *Megapodius* in dorsal (A, B) and ventral (C, D) aspects. A, C, *M. freycinet freycinet,* male, Halmahera, Northern Moluccas, USNM 557015; B, D, *M. molistructor,* Lifuka, Tonga, BPBM 165682. Scale bar = 10 mm.

Remarks.—This specimen is referred to *Megapodius molistructor* on the basis of its being much larger than any other species of *Megapodius* (Table 4), which is the only genus of Megapodiidae that occurs in Oceania. Intergeneric comparisons were not made. BPBM 165682 differs further from the coracoids of *M. pritchardi, M. freycinet,* and *M. wallacei* in having a less concave facies articularis humeralis. Although additional material is needed to determine with certainty whether the coracoid from Lifuka is conspecific with that of *M. molistructor,* this specimen does demonstrate that an extremely large species of megapode, approximately the size of *M. molistructor,* once lived on Lifuka.

The type series of *Megapodius molistructor,* an extinct species known otherwise only from New Caledonia (Balouet & Olson, 1989), does not include a coracoid. Nevertheless, BPBM 165682 is much larger than in *M. freycinet* and larger than would be expected for the coracoid of *M. alimentum.* In coracoidal measurements (Table 4), *M.* cf. *molistructor* from Lifuka is from 1.30+ to 1.45 times larger ($\bar{x}$ = 1.35+, n = 5) than the means for *M. freycinet freycinet.* This corresponds with ratios of the measurements of the scapula and ulna from the type series of *M. molistructor,* which are from 1.25 to 1.40 times larger ($\bar{x}$ = 1.33, n = 7) than the means for *M. freycinet freycinet* (Balouet & Olson, 1989:Table 3). No leg elements of *M.* cf. *molistructor* are available from Lifuka. The tarsometatarsus in *M. molistructor* from New Caledonia is much more massive than in *M. alimentum*

Table 4.—Measurements (in mm) of the coracoid in *Megapodius*, giving mean, range, and sample size. For sample sizes larger than 10, the mean is rounded to the nearest 0.05. CS = cotyla scapularis. FAC = facies articularis clavicularis. FAH = facies articularis humeralis. ILA = impressio ligamentum acrocoracoideum. F = female. M = male. U = sex unknown.

	Depth of FAC	Depth between ILA & FAH	Width of FAH	Length of FAH & CS	Minimum width of shaft
M. pritchardi	4.1	2.4	3.8	7.8	3.0
Niuafo'ou, Tonga (2U)	4.0–4.2	2.2–2.5	3.6–4.0	7.6–7.9	2.9–3.1
	2	2	2	2	2
M. cf. *molistructor*	7.9+	4.2	6.3+	13.6	5.7
BPBM 165682	1	1	1	1	1
Lifuka, Tonga (U)					
M. freycinet freycinet	5.95	2.90	4.85	10.20	4.20
Halmahera, Moluccas	5.4–6.4	2.6–3.4	4.6–5.2	9.5–11.2	3.6–4.6
(8M, 8F)	16	16	16	16	16
M. freycinet pusillus	6.4	2.9	4.8	10.3	4.5
Philippines (M)	1	1	1	1	1
M. freycinet gilberti	5.9	2.6	4.3	9.2	3.8
Celebes (1M, 1F)	5.6–6.2	2.4–2.7	1	9.1–9.2	3.8–3.9
	2	2		2	2
M. freycinet abbotti	6.2	3.0	4.8	10.1	4.2
Nicobar Islands (2M)	6.0–6.3	2.8–3.1	1	1	4.1–4.4
	2	2			2
M. wallacei	5.6	2.7	4.5	9.6	3.7
Halmahera, Moluccas (M)	1	1	1	1	1

(Fig. 2). Measurements of the tibiotarsus and tarsometatarsus of *M. alimentum* from Lifuka are, respectively, from 0.98 to 1.21 times larger ($\bar{x}$ = 1.10, n = 7) and 1.05 to 1.39 times larger ($\bar{x}$ = 1.16, n = 6) than the means for *M. freycinet freycinet,* while measurements of the femur and tarsometatarsus of *M. molistructor* from New Caledonia are, respectively, from 1.32 to 1.54 times larger ($\bar{x}$ = 1.39, n = 3) and 1.14 to 1.43 times larger ($\bar{x}$ = 1.31, n = 4) than the mean values for *M. freycinet freycinet.* The validity of these calculations is not likely to be compromised by a sexual dimorphism in size, which is extremely slight or non-existent in species of *Megapodius* (Mayr 1938, Amadon 1942).

Order Columbiformes
Family Columbidae
Genus *Ducula*

Two specimens are referred to the genus *Ducula* rather than other genera of pigeons from Polynesia or eastern Melanesia (*Columba, Ptilinopus, Caloenas, Gallicolumba, Goura, Didunculus*) because of these characters: coracoid—medio-ventral side of humeral end of shaft rounded, sulcus musculo supracoracoidei smooth and shallow, facies articularis sternalis medio-laterally expanded but dorso-ventrally compressed, impressio musculo sternocoracoidei deepest in medio-sternal corner; tibiotarsus—size and placement of prominent muscle scar on medio-distal surface of shaft, degree of concavity on the distal portion of shaft.

Ducula, undescribed species
Fig. 5

Material.—Tibiotarsus lacking both ends, BPBM 165685, Pit 0N0W, Layer IV (CU-III), Tongoleleka archeological site (To-Li), Lifuka, Ha'apai Group, Tonga. Tom Dye and field party Aug 1984.

Remarks.—This tibiotarsus is larger than in any other species of *Ducula* (Table 5).

Fig. 5. The tibiotarsus of *Ducula* in cranial (A–D) and caudal (E–H) aspects. A, E, Undescribed species, Lifuka, Tonga, BPBM 165685; B, F, *D. galeata,* Hanatekua Shelter No. 2 Archeological Site, Hiva Oa, Marquesas, BPBM 166055; C, G, *D. aurorae,* male, captive (original stock presumably from Makatea Island, Tuamotus), USNM 344776; D, H, *D. pacifica,* male, Rarotonga, Cook Islands, USNM 559586. Scale bar = 10 mm.

The proximo-ventral and disto-lateral portions of the shaft have smoother, more rounded surfaces than other species. This tibiotarsus is too fragmentary to be named, yet it represents one of the largest of all columbids, being exceeded in size only by the crowned pigeons of New Guinea (*Goura* spp.).

Ducula cf. *david* Balouet & Olson
Fig. 6

Referred material.—Nearly complete coracoid, lacking processus acrocoracoideus and part of facies articularis clavicularis, BPBM 165692, Pit 0N0W, Layer IV (CU-III), Tongoleleka archeological site (To-Li), Lifuka, Ha'apai Group, Tonga. Tom Dye and field party Aug 1984.

Remarks.—*Ducula david,* recently described from Wallis Island, was characterized mainly by being larger than any extant congeners (Balouet & Olson, 1987). Among living species of *Ducula,* the largest of which occurs on oceanic islands, only *D. galeata* of eastern Polynesia and *D. goliath* of New Caledonia approach the size of *D. david,* although even these species are slightly smaller and less robust (Table 6).

Ducula david is exceeded in size only by the huge extinct species noted above. Although comparable elements are not available for the undescribed species and *D. david,* comparisons of measurements of these

Table 5.—Measurements (in mm) of the tibiotarsus in *Ducula* and *Goura*, giving mean, range, and sample size. F = female. M = male. U = unknown.

	Length from distal end of fibular crest to distal knob	Length of fibular crest	Least width of shaft	Least depth of shaft
Ducula, undescribed sp.	57.4	23.3	5.5	4.8
Lifuka, Tonga (U)	1	1	1	1
D. galeata	39.7+	—	3.9	3.3
Nuku Hiva, Marquesas (M)	(est. 41–42)		1	1
	1			
D. galeata	40.5	—	4.3	3.3
Henderson Island (U)	(composite)		1	1
BPBM 160464, 160267				
D. galeata	41.5	—	4.2	3.6
Hiva Oa, Marquesas (U)	1		1	1
BPBM 166055				
D. goliath	27.1	12.7	4.3	3.8
New Caledonia (1M, 2F)	26.2–28.1	11.7–13.6	4.1–4.7	3.6–4.1
	3	3	3	3
D. aurorae	26.6	10.9	3.9	3.0
Captive (M)	1	1	1	1
D. pacifica	30.9	11.0	3.6	2.9
Niuafo'ou, Rarotonga	30.2–31.8	10.9–11.2	3.3–3.7	2.8–3.0
(1M, 1F, 1U)	3	3	3	3
D. oceanica	30.0	11.2	3.0	2.5
Palau, Ponape (2U)	28.5–31.4	11.0–11.4	3.0–3.1	2.4–2.6
	2	2	2	2
D. aenea	28.4	14.2	4.1	3.3
Philippines (F)	1	1	1	1
D. perspicillata	28.9	13.6	3.9	3.2
Halmahera, Moluccas	28.2–29.6	13.2–14.1	3.9	3.0–3.4
(1M, 1F)	2	2	2	2
D. bicolor	38.5	13.0	3.7	3.0
Halmahera, Moluccas (M)	1	1	1	1
D. luctuosa	28.2	13.9	3.5	3.1
Celebes (F)	1	1	1	1
D. spilorrhoa	25.2	14.2	3.2	2.9
Australia (U)	1	1	1	1
D. badia	23.1	13.1	3.4	2.8
Thailand (M)	1	1	1	1
D. pinon	29.4	14.0	4.0	3.1
Captive (M)	1	1	1	1
D. radiata	19.4	10.7	3.1	2.4
Celebes (M)	1	1	1	1
Goura victoria	68.0	24.7	6.7	5.9
Captive (M)	1	1	1	1

species with those of *D. galeata* and *D. goliath* indicate that the undescribed species is larger than *D. david* (Tables 5 and 6 herein; Balouet & Olson, 1987: Table 1). In particular, the tibiotarsus of the undescribed species is 1.40 times longer than that of *D. galeata*, whereas the holotypical tarsometatarsus of *D. david* from Wallis Island is only


165692
165692
160956
559586
A
B
C
D
E
F
G
H

1.01 times longer than that of *D. galeata* and 1.12 times longer than that of *D. goliath.* These ratios correspond well with those of the coracoid in *D.* cf. *david* from Lifuka, which is 1.07 times longer than that in *D. galeata* and 1.12 times longer than that in *D. goliath.* The amount of sexual dimorphism in size is poorly understood in oceanic species of *Ducula* owing to the worldwide scarcity of skeletons. In measurements of *D. goliath,* the male is consistently larger than the female (Tables 5 and 6), although these are captive individuals that may not be reliable indicators of the size of wild birds.

No skeletons were available for *D. latrans* of Fiji. Based upon measurements of skins (duPont 1976:83–85), *D. latrans* is approximately the same size as *D. aurorae* or *D. pacifica,* and thus would be much smaller than *D. david.*

Ducula pacifica (Gmelin)

Referred material.—Ulna lacking both ends (BPBM 165676), Pit 126N0W, Layer III (CU-IIb), Tongoleleka archeological site (To-Li), Lifuka, Ha'apai Group, Tonga. Tom Dye and field party Aug 1984.

Remarks.—The curvature of the shaft and the prominent papillae remigiales caudales refer this ulna to the Columbidae. The specimen agrees in size and other features with the ulna of *Ducula pacifica.* Each of the other three species of columbids reported here is much larger than *D. pacifica,* which is the only species of columbid (other than *Gallicolumba stairii* and species of *Ptilinopus,* which are very small) surviving on Lifuka or anywhere else in Tonga.

Genus *Caloenas*

Among the bird bones from the Tongoleleka Site is another coracoid of a large columbid. This specimen, slightly smaller than in *D.* cf. *david* (Table 6), is referred to the genus *Caloenas* rather than to *Ducula* or other pertinent genera of columbids because of these characters: greater pneumaticity in humeral end of sulcus musculo supracoracoidei; facies articularis humeralis protrudes more ventrad from surface of shaft; sharp medio-ventral edge of humeral end of shaft; in medial aspect, portion of shaft between cotyla scapularis and facies articularis clavicularis faces more perpendicularly (less diagonally); facies articularis clavicularis deeper.

Caloenas cf. *canacorum* Balouet & Olson
Fig. 7

Referred material.—Humeral end of coracoid, including facies articularis humeralis and cotyla scapularis, BPBM 165678, Pit 0N20E, Layer II (CU-II), Tongoleleka archeological site (To-Li), Lifuka, Ha'apai Group, Tonga. Tom Dye and field party Aug 1984.

Remarks.—*Caloenas canacorum* is an extinct species recently described from late Holocene fossils (sternum, coracoids, scapula, and humerus) from New Caledonia (Balouet & Olson, 1989). Although direct comparison of the holotype coracoid of *C. canacorum* with BPBM 165678 was not possible except in photographs (Fig. 7), BPBM 165678 is referred to *C.* cf. *canacorum* because of similarity in qualitative generic characters and in size, being significantly larger than in *C. nicobarica,* the only living species in this distinctive genus (Table 6).

Discussion

Although the detailed implications of these findings will be reported elsewhere, a

←

Fig. 6. The coracoid of *Ducula* in dorsal (A–D) and ventral (E–H) aspects. A, E, *D.* cf. *david,* Lifuka, Tonga, BPBM 165692; B, F, *D. galeata,* Hanatekua Shelter No. 2 archeological site, Hiva Oa, Marquesas, BPBM 166056; C, G, *D. aurorae,* male, captive (original stock presumably from Makatea Island, Tuamotus), USNM 344776; D, H, *D. pacifica,* male, Rarotonga, Cook Islands, USNM 559586. Scale bars = 10 mm.

Table 6.—Measurements (in mm) of the coracoid in *Ducula* and *Caloenas*, giving mean, range, and sample size. The values for *D. david* from Wallis Island are estimations extrapolated from similar measurements in Table 1 of Balouet & Olson (1987). The values for *C. canacorum* from New Caledonia are taken, either directly or from extrapolated estimations, from Balouet & Olson (1989). F = female. M = male. U = sex unknown.

	Maximum length	Length from sternal facet to sternal end of facies articularis humeralis	Depth of humeral end	Length of facies articularis humeralis	Width of facies articularis humeralis	Least depth of shaft between cotyla scapularis and processus acrocoracoideus	Least depth of shaft	Least width of shaft	Width of sternal end
D. cf. *david*	48.0+	41.8	—	—	5.5+	6.9	4.9	5.1	15.5+
Lifuka, Tonga (U)	(est. 53)	1			1	1	1	1	(est. 21)
	1								1
D. david	—	—	—	—	—	—	ca. 4.2	—	—
Wallis Island (U)							1		
D. galeata	49.6	38.2	5.6	7.6	4.3	5.0	3.9	3.8	18.0
Hiva Oa, Marquesas	1	1	1	7.1–8.0	4.0–4.6	4.9–5.2	1	1	1
BPBM 166056 (U)				2	2	2			
D. goliath	47.6	35.8	6.1	7.2	4.8	5.3	4.2	4.4	18.7
New Caledonia	44.9–49.6	34.1–37.4	5.5–6.5	6.9–7.4	4.3–5.4	5.0–5.6	4.0–4.7	4.1–4.8	17.4–20.1
(1M, 2F)	3	3	3	2	2	2	3	3	3
D. aurorae	41.2	31.1	4.6	6.2	4.0	—	3.6	3.7	15.3
Captive (M)	1	1	1	1	1		1	1	1
D. pacifica	37.8	29.4	4.0	5.5	3.6	3.9	2.8	2.8	14.2
Gilberts, Niuafo'ou,	36.3–41.0	28.4–32.2	3.9–4.1	5.3–5.9	3.2–3.9	3.5-4.3	2.5–3.0	2.4–3.1	13.4–15.6
Rarotonga (2M, 1F, 1U)	4	4	4	4	4	4	4	4	4
D. oceanica	34.9	27.0	3.8	4.7	3.1	3.6	2.8	2.6	13.6
Palau, Ponape	32.7–36.5	25.1–28.2	3.5–4.0	4.5–5.0	3.0–3.3	3.6–3.7	2.6–3.0	2.4–2.8	13.4–13.8
(3U)	3	3	3	3	3	2	3	3	2
D. myristicivora	47.8	34.9	5.7	8.0	—	—	4.0	4.2	—
Captive (M)	1	1	1	1			1	1	
D. aenea	45.2	34.1	4.7	7.6	4.0	5.0	4.0	3.8	17.3
Philippines (F)	1	1	1	1	1	1	1	1	1
D. perspicillata	46.6	35.0	5.4	7.6	4.4	4.8	4.0	4.0	18.5
Halmahera, Moluccas	45.9–47.2	34.4–35.5	5.2–5.5	7.2–8.1	4.4–4.5	4.7–5.0	3.8–4.2	3.9–4.1	18.4–18.6
(1M, 1F)	2	2	2	2	2	2	2	2	2

Table 6.—Continued.

	Maximum length	Length from sternal facet to sternal end of facies articularis humeralis	Depth of humeral end	Length of facies articularis humeralis	Width of facies articularis humeralis	Least depth of shaft between cotyla scapularis and processus acrocoracoideus	Least depth of shaft	Least width of shaft	Width of sternal end
D. bicolor	41.5	31.0	4.5	7.2	4.0	4.6	3.6	3.5	—
Halmahera, Moluccas (M)	1	1	1	1	1	1	1	1	
D. luctuosa	43.0	33.0	5.0	7.1	4.1	—	3.7	3.8	—
Celebes (F)	1	1	1	1	1		1	1	
D. spilorrhoa	40.7	30.5	4.8	7.0	4.0	—	3.7	3.8	—
Australia (U)	1	1	1	1	1		1	1	
D. badia	42.9	32.6	4.5	6.3	3.9	—	3.5	3.8	—
Thailand (M)	1	1	1	1	1		1	1	
D. pinon	48.6	36.7	5.4	7.0	4.5	—	4.0	3.9	—
Captive (M)	1	1	1	1	1		1	1	
D. radiata	38.9	29.3	3.8	6.0	3.0	3.6	2.9	2.9	14.4
Celebes (M)	1	1	1	1	1	1	1	1	1
Caloenas nicobarica	44.8	33.7	5.1	7.4	4.7	5.1	3.6	3.6	15.8
Halmahera, Moluccas	43.5–46.5	32.3–34.8	4.8–5.5	6.8–7.9	4.4–5.0	4.6–5.5	3.3–3.8	3.2–4.0	14.9–16.8
(5F)	5	5	5	5	5	5	5	5	5
C. canacorum	59.2	—	8.2	—	—	—	—	—	—
New Caledonia (2U)	59.0–59.4		7.2–9.1						
	2		2						
C. cf. *canacorum*	—	—	6.5+	8.9	5.2	6.1	—	—	—
Lifuka, Tonga (U)			1	1	1	1			
BPBM 165678									

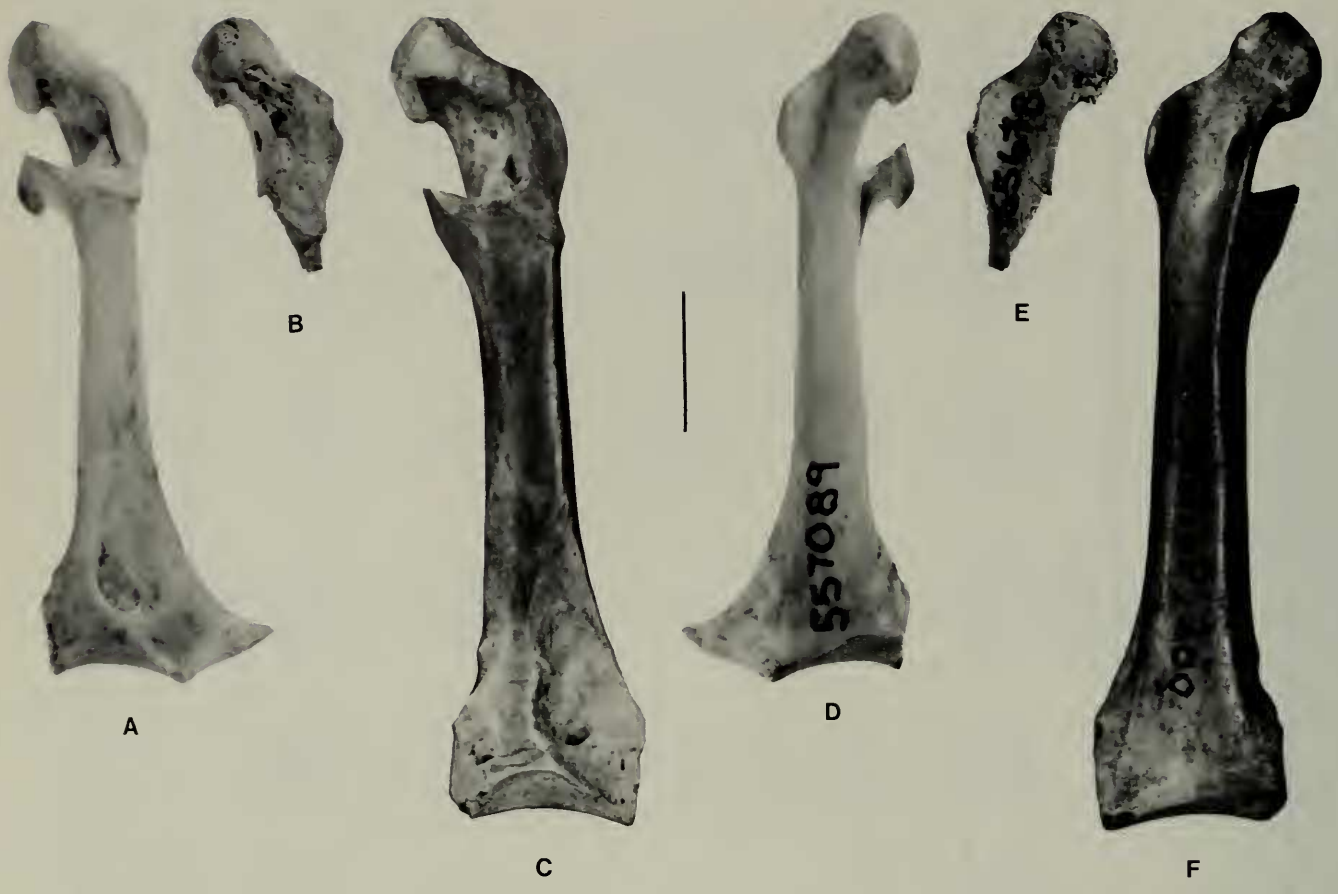

Fig. 7. The coracoid of *Caloenas* in dorsal (A–C) and ventral (D–F) aspects. A, D, *C. nicobarica,* female, Halmahera, Northern Moluccas, USNM 557089; B, E, *Caloenas* cf. *canacorum,* Lifuka, Tonga, BPBM 165678; C, F, *C. canacorum,* paratype, New Caledonia, MNHN 300. Scale bar = 10 mm.

few comments are pertinent here. The undescribed species of *Ducula* is of unknown interspecific relationships. The other extinct birds from Lifuka are related to species found west or north of Tonga. It seems likely that all of these species, or closely related ones, once occurred through much of the region of New Caledonia, Vanuatu, Fiji, Tonga, and Samoa. *Megapodius molistructor* and *Caloenas canacorum* are known only from New Caledonia and tentatively from Lifuka. *Megapodius alimentum* and the undescribed species of *Ducula* are known only from Lifuka, although there is no reason to believe that they were confined to that island. Aside from Lifuka, *D. david* is known from Wallis (Uvea) Island, which is north of Lifuka, between Samoa and Fiji.

The late Holocene extinction of two species of megapodes and three species of pigeons on Lifuka shows that there has been a significant loss of birds in western Polynesia since the arrival of man. Numerous extinctions have been documented by fossil records from more remote parts of Polynesia, such as Hawaii (Olson & James 1982a, b), Marquesas (Steadman, in press), Henderson Island (Steadman & Olson 1985), Cook Islands (Steadman 1985, in press), and New Zealand (Cassels 1984). More excavation is needed in Tonga and Samoa. Based upon the limited record available, the degree of avian extinction in western Polynesia may have been just as severe as that from elsewhere in Polynesia.

The fossils from Lifuka indicate that two species of *Megapodius* once occurred there. *Megapodius pritchardi,* restricted to the isolated Tongan island of Niuafo'ou, is the only species of megapode that survives anywhere in Polynesia, although we presently do not know to what extent the natural range of

megapodes has been reduced by human impact. The widespread *M. freycinet* reaches the eastern limit of its range in Vanuatu (New Hebrides). That the absence of megapodes in the Fijian region may be an artifact of human disturbance was noted by Olson (1980) and confirmed several years ago by our examination of bones of *Megapodius* (species undetermined) from an archeological site on Lakeba, Lau Group, Fiji (reported in Gibbons & Clunie 1986). Elsewhere in the western Polynesian and Melanesian region, extinct megapodes (species undetermined) have been reported from as yet unconfirmed historical accounts in the Kermadec Islands (Lister 1911), archeological sites on Tikopia (Kirch & Yen 1982: 282; Green 1976), an egg collected in 1847 from Samoa (island undetermined; Gray 1862), and an egg collected before 1862 from an undetermined island in the Ha`apai Group of Tonga (Gray 1862, 1864). Oates (1901) referred the last two specimens to *M. pritchardi,* a determination that should be reconfirmed.

A better understanding of the systematics and natural distribution of megapodes in Oceania depends upon the reexamination of historic specimens and documents, and more fully upon the discovery and study of bones from prehistoric sites on many additional islands. It now seems likely that one to three species of megapode occurred on most or all islands of eastern Melanesia and western Polynesia before the arrival of humans. Four species of megapodes still exist, for example, on the Papuan island of Misool (Ripley 1960).

Columbids also have suffered much extinction in Oceania. The hunting of pigeons by prehistoric Tongans was extensive and highly organized (McKern 1929:19–27). *Ducula pacifica* is the largest pigeon known historically from anywhere in Tonga, where it is found essentially throughout the group. Fossils from Tongoleleka represent three additional species of columbids, each extinct and larger than *D. pacifica.* Although it may seem remarkable that four large species of columbids, including three species of *Ducula,* once lived on Lifuka, we really do not yet know the natural (=pre-human) distribution and diversity of Pacific columbids. From Mangaia in the Cook Islands, for example, late Holocene fossils represent five species of columbids where none exists today (Steadman 1985, 1989).

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